

Grasshopper Herbivory Affects Native Plant Diversity and Abundance in a Grassland Dominated by the Exotic Grass *Agropyron cristatum*

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Abstract

The indirect effects of native generalist insect herbivores on interactions between exotic and native grassland plants have received limited attention. Crested wheatgrass (*Agropyron cristatum*) is the most common exotic rangeland grass in western North America. Crested wheatgrass communities are resistant to colonization by native plant species and have strong competitive effects on native species, imposing problems for the restoration of native grasslands. Grasshoppers are generalist herbivores that are often abundant in Crested wheatgrass-dominated sites in the northern Great Plains. We conducted two experiments in a Crested wheatgrass-dominated grassland in western North Dakota to test the hypothesis that grasshopper herbivory influences local Crested wheatgrass community

composition by impeding native seedlings. Grasshopper herbivory negatively affected the species richness, abundance, and Shannon diversity of native plants in 3 of 4 years. Although additional research is needed to determine if grasshoppers actively select native plants, the effects of grasshopper herbivory may be an important consideration in the restoration of Crested wheatgrass areas. Our findings illustrate the importance of understanding the impact of native generalist invertebrate herbivores on the relationships between exotic and native plants.

Key words: Crested wheatgrass, generalist herbivore, grasshoppers, indirect effects, plant community.

Introduction

Exotic plant species can negatively affect native plants directly through competition (Bakker & Wilson 2001; Vilà & Weiner 2004) or indirectly by modifying interactions between native plants and their environment (Lau & Strauss 2005; Thelen et al. 2005). Selective herbivory by insects can affect plant community structure (Belovsky & Slade 2000; Carson & Root 2000; Hambäck & Beckerman 2003), influence the competitive dynamics between plants (Hambäck & Beckerman 2003; Haag et al. 2004; Thelen et al. 2005), and modify invasion dynamics (Brown 1994; Maron & Vilà 2001; Lau & Strauss 2005). However, indirect effects of native insect herbivores on the interactions between introduced grasses and native grassland plants have received relatively limited attention (Callaway et al. 1999; Maron & Vilà 2001; Lau & Strauss 2005). In addition, few studies have examined how insect herbivory affects seedling survival or recruitment (Hulme 1994).

Crested wheatgrass (*Agropyron cristatum*) is the most common exotic rangeland grass in western North America and had been planted on an estimated 6–10 million ha of the Great Plains as of 1996 (Pyke 1990; Lesica & DeLuca 1996). In the Great Plains, much formerly native prairie was planted to Crested wheatgrass in the 1920s and 1930s to reduce soil erosion in abandoned agricultural lands (Lorenz 1986; Onsager 2000). Crested wheatgrass continues to be planted as part of the Conservation Reserve Program in the western United States (Lloyd & Martin 2005). It is commonly used for early season livestock grazing in the northern Great Plains because it begins to grow earlier than most native grasses (Pyke 1990; Uresk & Bjugstad 2000; Hansen & Wilson 2006). Crested wheatgrass populations are resistant to colonization by native plant species (Christian & Wilson 1999). They also have strong competitive effects on native species (Bakker & Wilson 2001). Areas with high densities of Crested wheatgrass have reduced native plant species diversity (Heidinga & Wilson 2002) and reduced avian nesting success (Lloyd & Martin 2005). Crested wheatgrass frequently invades adjacent native grass prairie (Klement et al. 2001; Heidinga & Wilson 2002; Henderson & Naeth 2005), perhaps due to its high rate of seed production (Heidinga & Wilson 2002; Ambrose & Wilson 2003). These characteristics of Crested wheatgrass impose a problem for the restoration and maintenance of native grasslands (Bakker & Wilson 2001; Ambrose & Wilson 2003).

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Grasshoppers are common insect herbivores in grasslands worldwide (Branson et al. 2006), and their feeding patterns can have important impacts on local plant abundance and community structure (Parker 1985; Thompson et al. 1996; Belovsky & Slade 2000). For example, high densities of the specialist grasshopper Snakeweed grasshopper (*Hesperotettix viridis*) led to lower levels of fecundity and high levels of mortality in Snakeweed (*Gutierrezia* spp.) (Parker & Salzman 1985; Thompson et al. 1996). In contrast to the majority of herbivorous insects, most grasshopper species tend to be generalist feeders that consume a variety of unrelated plant species (Chapman 1990; Chapman & Sword 1997). Some grasshoppers are specialized to a degree, particularly on grasses, but even grass-feeding species tend to be generalists and consume an array of species within this plant group (Mulkern et al. 1969; Joern 1979). Temporal changes in plant community composition (Bernays & Chapman 1970; Banfill & Brusven 1973; Bernays et al. 1976) or characteristics such as leaf toughness that change with plant phenology (Clissold et al. 2006) may also influence the selection of multiple plants by grasshoppers.

Grasshopper densities are often high in areas dominated by Crested wheatgrass. Over a 5-year study in the northern Great Plains, grasshopper days, an index of seasonal abundance, averaged nearly five times higher in Crested wheatgrass sites than in native prairie sites (Onsager 2000). Higher densities on Crested wheatgrass sites were hypothesized to result from decreased ground cover and reduced plant canopy shading creating favorable thermal conditions for development. Given that grasshoppers are generalist herbivores, grasshopper herbivory on plants other than Crested wheatgrass could play an important role in mediating local plant community composition. As such, the effects of grasshopper herbivory may be an important consideration in the restoration of Crested wheatgrass areas in the northern Great Plains.

Restoration ecologists have largely focused on the competitive abilities of Crested wheatgrass in relation to native plant species to explain the persistence and invasion of Crested wheatgrass (Bakker & Wilson 2001), and it is only recently that the potential ecological effects of herbivory in Crested wheatgrass-dominated communities have been considered. Wilson and Pärtel (2003) hypothesized that grazing Crested wheatgrass could reduce its competitive ability and found that clipping Crested wheatgrass to simulate livestock grazing increased native plant cover. The impacts of smaller herbivores such as grasshoppers on the abundance and diversity of native plants in Crested wheatgrass-dominated sites have not been examined. The effects of grasshopper herbivory may differ in important ways from those of vertebrates because the insects are present throughout the growing season and feed at a smaller spatial scale.

Field observations suggested that grasshoppers in Crested wheatgrass-dominated habitats commonly fed on later emerging native plant seedlings (G. Sword 2001, personal

observation). Given the potential community-level effects of this pattern of herbivory, we set out to test the hypothesis that grasshopper herbivory influences Crested wheatgrass community composition by impeding native seedlings.

Methods

Study System

The study site was located in a pasture on the Little Missouri National Grassland (U.S. Forest Service) in McKenzie County, North Dakota, U.S.A. (lat 47°39.466'N, long 103°51.301'W). Vegetation in the pasture was dominated by Crested wheatgrass that was likely planted in the 1930s (Onsager 2000; Uresk & Bjugstad 2000). Livestock grazing in the pasture historically occurred during the month of May, with additional grazing after 15 October in some years (Onsager 2000). Peak summer grasshopper densities at the site averaged 32/m² between 1993 and 1998 (Onsager 2000). Peak grasshopper densities ranged between 3 and 21/m² from 2002 to 2005. Between 2002 and 2005, the most common early to mid-summer grasshopper species at the site were Whitewiskered grasshopper (*Ageneotettix deorum*), Little spurthroated grasshopper (*Melanoplus infantilis*), and Migratory grasshopper (*M. sanguinipes*). *Ageneotettix deorum* is a grass and sedge feeder, whereas both *M. infantilis* and *M. sanguinipes* are generalist species that feed on both grasses and forbs (Pfadt 2002).

Experimental Design

We conducted a single-field season pilot experiment in 2002 and subsequently conducted a similar 3-year field experiment from 2003 through 2005 within 50 m of the first experiment using a different generalist grasshopper species. For each experiment, a visually uniform site was chosen, and a small grazing exclosure, approximately 11 × 11 m, was established using livestock panels. The exclosure remained in place for the duration of an experiment. Treatments consisted of grasshopper herbivory and grasshopper exclusion (no herbivory).

Cage plots measuring 1 × 1 m were laid out within the exclosures. Treatment replication level was 10 in 2002 and 9 from 2003 to 2005, and treatments were randomly assigned to cages. Before initiating an experiment, vegetation surveys were conducted on each cage plot prior to placing cages over the vegetation in early June. Rectangular frames (0.25 × 1 m) were used to determine the presence and abundance of non-Crested wheatgrass vegetation within each quarter of a plot (Bullock 1996). Individual plants of all native forb species were counted, and the values from the four subplots were combined. Because it is difficult to distinguish between individual plants for some grasses (Elzinga et al. 2001) and because native grasses were too rare to assess in each subplot, native grass species were recorded as present or absent within

a given cage (Bullock 1996). Species richness and abundance (number/1-m² plot) of native plants did not differ significantly between treatments at the start of either experiment (analysis of variance [ANOVA] models, all $p > 0.4$). Following the initial vegetation survey, cages were placed over all vegetation plots. The 1 × 1 × 0.5-m cages were constructed of Lumite insect netting (SI Corporation, Gainesville, GA, U.S.A.), with a zipper on the side of the cage and 15-cm-wide polyester flaps at the base that laid flat around the exterior of the cage. The cages were placed over a frame composed of polyvinyl chloride water pipe, fastened to the ground with spikes driven through grommet holes in the flaps at all corners, and sandbags were placed continuously around the cage on the flaps to prevent grasshoppers from escaping. Cages were used for both treatments to control for cage effects on microclimate and precipitation. Similar cages have been used in numerous studies with grasshoppers (Joern & Klucas 1993; Belovsky & Joern 1995; Belovsky & Slade 2000; Schmitz 2004).

Herbivory treatment cages were randomly assigned and stocked with two grasshopper species, the most common grass feeder and the most common generalist at the site. Insects were collected in the immediate vicinity to ensure that they had been exposed to Crested wheatgrass. The two species were stocked at equal densities in the herbivory cages, with a total density of 30 grasshoppers/cage. The cage density was within the range of grasshopper densities previously observed at the site (Onsager 2000). The species of generalist grasshopper stocked in cages differed between the two experiments because the proportional species composition of *M. sanguinipes* at the site declined following 2002. In the 2002 experiment, herbivory cages were maintained with *A. deorum* and *M. sanguinipes*, whereas *A. deorum* and *M. infantilis* were utilized for the 2003–2005 experiment. Densities of grasshoppers were assessed in herbivory cages every 3 weeks, and grasshoppers were added as necessary to maintain the density of 30 grasshoppers/cage at the same species composition. Herbivory exclusion cages were checked periodically to ensure that no grasshopper hatching occurred inside the cages.

The late-season vegetation surveys occurred before most native plants had senesced (late July or August), but because vegetation was not monitored continuously, we cannot eliminate the possibility that some plants may have dried up prior to sampling. Vegetation was surveyed as described above, and the cages were removed to allow plants to be accurately counted. After late-summer vegetation surveys were conducted in 2003, the herbivory exclusion treatment cages were replaced until grasshopper densities declined to low levels outside the cages. Late-summer grasshopper densities in 2004 and 2005 were lower than three grasshoppers/m², so cages were not reinstalled following the final vegetation surveys. It was not always possible to identify forbs to genus or species because they were often either immature or partially

eaten. In these cases, matching plants were harvested outside the cages and placed in a collection to allow consistent recording of unknown plants throughout all cages. Documented forbs at the site included Prairie sagewort (*Artemisia frigida*), Thymeleaf sandmat (*Euphorbia serpyllifolia*), Scarlet globemallow (*Sphaeralcea coccinea*), Winter fat (*Ceratoides lanata*), Blue flax (*Linum lewisii*), Woolly plantain (*Plantago patagonica*), Prairie wild rose (*Rosa arkansana*), Pussytoes (*Antennaria* spp.), Scurfpea (*Psoralea* spp.), Parsley (*Lomatium* spp.), Milkvetch (*Astragalus* spp.), and Draba (*Draba* spp.). Native grasses and sedges occurring at the site included Blue grama (*Bouteloua gracilis*), Mat muhly (*Muhlenbergia richardsonis*), Needle and thread (*Stipa comata*), Prairie junegrass (*Koeleria pyramidata*), and Threadleaf sedge (*Carex filifolia*). Other non-native species occurring at the site included Yellow sweetclover (*Melilotus officinalis*) and Dandelion (*Taraxacum officinale*).

Statistics

ANOVA models were used to examine grasshopper herbivory, year, and year × herbivory treatment effects on numerical native plant abundance, native forb species richness, and Shannon diversity index. Statistics were not used to assess grass species richness or abundance due to the rarity of native grasses in all plots. One-way ANOVA models were used to examine the data from the 2002 experiment. Abundance results were square root transformed prior to analysis to meet normality assumptions (Quinn & Keough 2002). Cage mean values were used for all analyses. For the 2003–2005 experiment, repeated measures ANOVA models using the mixed procedure (SAS Institute, Inc. 2003) were used to examine treatment differences because the same cage sites were used for all 3 years of the experiment. Pairwise differences in native plant numerical abundance were assessed using a multiple comparison test. When a significant year × treatment interaction occurred, a posteriori simple main effects of grasshopper herbivory on species richness and Shannon diversity were examined separately for each year (Quinn & Keough 2002). The examination of simple main effects allowed an examination of the effects of grasshopper herbivory separate from yearly climatic variation. Systat 11 (Systat Software, Inc. 2004) and SAS 9.1 (SAS Institute, Inc. 2003) were used for all statistical analyses.

Results

Forbs dominated among the non-Crested wheatgrass species found in the cages. Grasshopper herbivory negatively affected the numerical abundance, species richness, and Shannon diversity of native forb species (Table 1; Fig. 1) in the single-year experiment conducted in 2002. Grasshopper herbivory also negatively affected the numerical abundance of native forbs over the 3-year experiment from 2003 to 2005, with abundance varying significantly

Table 1. (A) ANOVA results from the 2002 grasshopper herbivory cage experiment and (B) repeated measures ANOVA results from the 2003–2005 experiment for native forb abundance (number/1-m² cage), native plant species richness, and Shannon diversity index.

Dependent	Effect	df	F	p
A.				
Abundance	Herbivory	1, 18	6.18	0.02
Species richness	Herbivory	1, 18	7.79	0.01
Shannon diversity	Herbivory	1, 18	4.94	0.04
B.				
Abundance	Herbivory	1, 16	14.18	<0.002
	Year	2, 32	20.47	<0.001
	Interaction	2, 32	2.34	0.11
Species richness	Herbivory	1, 16	6.94	0.018
	Year	2, 32	16.70	<0.001
	Interaction	2, 32	4.27	0.023
Shannon diversity	Herbivory	1, 16	6.07	0.025
	Year	2, 32	2.76	0.078
	Interaction	2, 32	4.88	0.014

among years (Table 1). The abundance of native forbs was significantly lower with grasshopper herbivory in both 2003 and 2004 (Fig. 2).

There was a significant year \times treatment interaction effect on the species richness of native plants (Table 1). The interaction resulted from very low species richness in all plots during 2004 when species richness averaged approximately three species/plot in both treatments (Fig. 2). Based on a posteriori simple main effect tests, species richness was significantly lower with grasshopper herbivory in both 2003 and 2005 but not in 2004 (Fig. 2).

There was a similar significant treatment \times year interaction on Shannon diversity index, with Shannon diversity similar between treatments in 2004 when species richness was low (Fig. 2). Based on a posteriori simple main effect tests, Shannon diversity was significantly lower in grasshopper herbivory treatment cages in both 2003 and 2005 but not in 2004 (Fig. 2).

In the 2002 experiment, native grasses occurred in 4 of 10 cages with herbivory and in 3 of 10 herbivory exclusion cages during the late-summer vegetation survey. During the 2003–2005 experiment, native grasses occurred in three of nine cages in each treatment in 2003. Only one of the three grasshopper herbivory cages with native grasses in 2003 contained native grasses in 2005. By contrast, six of nine herbivory exclusion treatment cages contained native grasses in 2005.

Discussion

Grasshopper herbivory in a Crested wheatgrass-dominated community led to a reduction in native forb species richness, diversity, and abundance in 3 of 4 years of this study. In many native grassland systems, herbivores tend to increase plant diversity; however, negative effects are

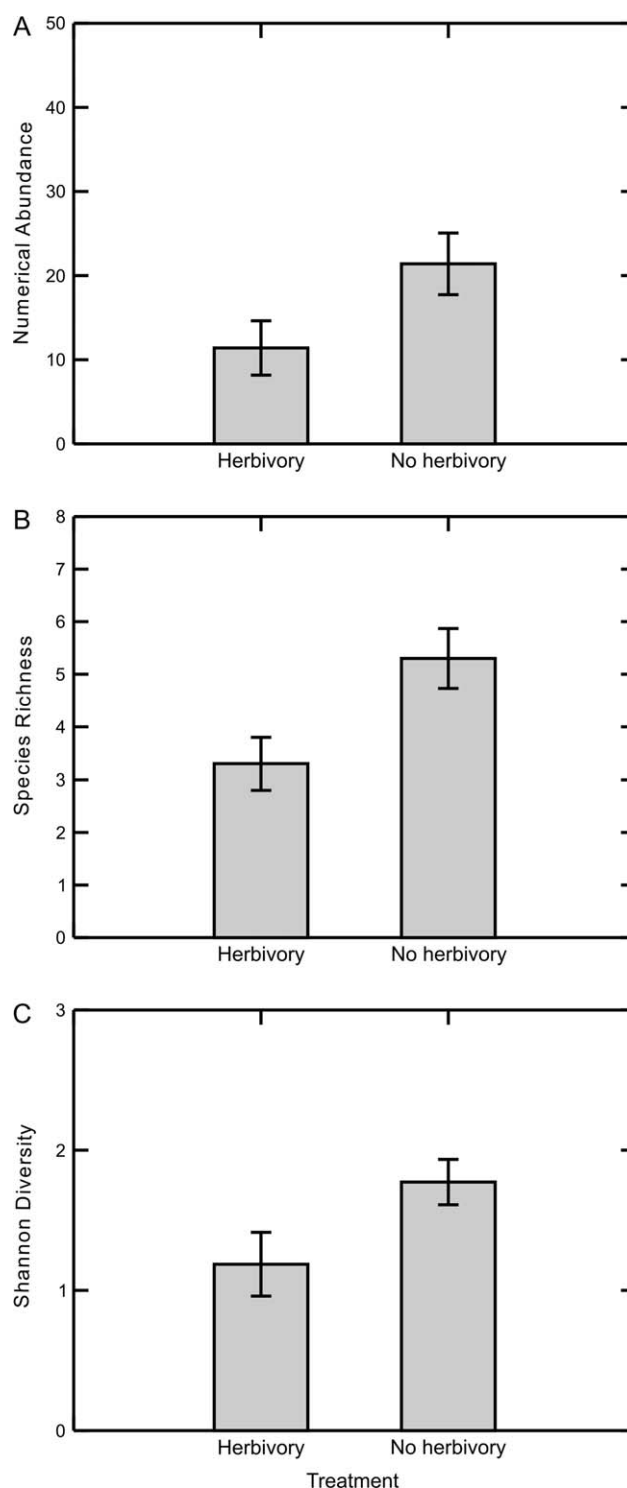


Figure 1. (A) Native forb abundance (number/1-m² cage), (B) native plant species richness, and (C) Shannon diversity in herbivory and herbivory exclusion (no herbivory) treatment cages for the 2002 experiment. Values are $\bar{X} \pm \text{SE}$.

more commonly observed in more arid grassland ecosystems (Olf & Ritchie 1998). Herbivory by grasshoppers led to a reduction in the number of countable plants by

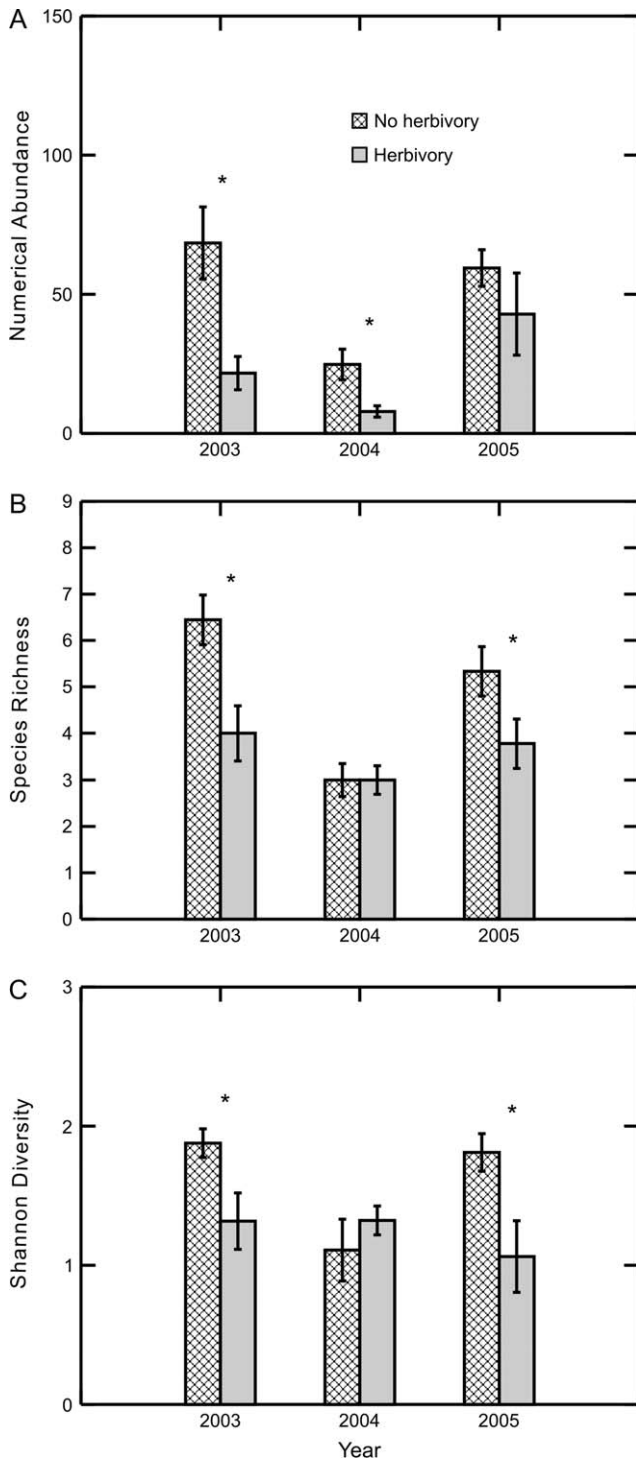


Figure 2. (A) Native forb abundance (number/1-m² cage), (B) native plant species richness, and (C) Shannon diversity index in herbivory and herbivory exclusion (no herbivory) treatment cages for each year in the 2003–2005 experiment. Values are $\bar{X} \pm \text{SE}$. For numerical abundance, asterisks indicate significant differences between treatments within a year (Bonferroni, $p < 0.05$). For species richness and Shannon diversity, asterisks indicate significant differences between treatments for a given year based on a posteriori simple main effect tests ($p < 0.05$).

removing all aboveground biomass, but these data do not establish that all plants eaten to ground level were killed. Mature grasses would be expected to withstand severe defoliation by grasshoppers without leading to mortality (Burlinson & Hewitt 1982; Thompson & Gardner 1996). However, the seedlings of both grasses and forbs could be more vulnerable to grasshopper herbivory. Although statistical hypothesis testing was not feasible due to the unfortunate rarity of native grasses, the number of herbivory exclusion cages containing native grasses increased from three to six, whereas the number in the herbivory cages declined from three to one over the course of the experiment. It is important to note that native grasses did not disappear from any cages in the control treatment during the experiment or appear in any cages in the grasshopper herbivory treatment during the last year of the experiment. This pattern suggests that the elimination of grasshopper herbivory may have favored the establishment of native grasses. Because plants presumably have lower competitive abilities when fed on by herbivores (Thelen et al. 2005), herbivory by grasshoppers on native plant seedlings could also make these plants more vulnerable to competition from Crested wheatgrass. Additional research on grasshopper host plant selection behaviors will be required to determine if grasshoppers actively select native plants once Crested wheatgrass becomes mature or if the results of this study are due to uniformly high rates of herbivory on both Crested wheatgrass and native plant species.

Maron and Vilà (2001) proposed that native generalist herbivores could facilitate more than inhibit the invasion of exotic plants. Our results suggest that vertebrate and invertebrate herbivores could have different effects on the competitive dynamics in this system. Clipping Crested wheatgrass to simulate livestock grazing led to decreased Crested wheatgrass cover and increased native plant cover, which was hypothesized to result from the reduced competitive ability and seed production of Crested wheatgrass (Wilson & Pärtel 2003; Hansen & Wilson 2006). In contrast to the hypothesized effects of vertebrate grazing, grasshopper herbivory caused a decrease in plant diversity. Grasshopper herbivory differs in important ways from clipping or livestock grazing. These insects are present at a site throughout the summer, supplying a longer-term herbivory effect than a single clipping event or relatively short-duration livestock rotation. In addition, although livestock are selective foragers, individual grasshoppers select and feed on plants at a much smaller scale than livestock and thus have the potential to more strongly influence the survival of native plant seedlings. Although grasshopper herbivory may have weakened the competitive abilities of Crested wheatgrass, the direct effects of grasshopper herbivory on native plants appear to be more important in this system.

The observed effects of grasshopper herbivory on native plant abundance and diversity are likely to apply to Crested wheatgrass-dominated areas across the northern

Great Plains and may be more broadly relevant in other ecosystems where generalist insect herbivores are abundant in areas dominated by exotic plants. In addition, the results expand our understanding of how generalist herbivores affect the success and invasion of exotic plants (Agrawal & Kotanen 2003; Hambäck & Beckerman 2003; Maron & Vilà 2001). Crested wheatgrass-dominated sites in the northern Great Plains often have high grasshopper densities, with lower species diversity than on native prairie sites (Branson, unpublished data; Onsager 2000). Grasshopper densities are known to fluctuate in a cyclical pattern (Belovsky 2000; Joern 2000; Branson et al. 2006), and although grasshopper densities were maintained at higher densities in cages than occurred in the field from 2002 through 2005, they were still well within the long-term density range found at the site (Onsager 2000). As such, our results mainly address the plant community-level effects of relatively intense herbivory by grasshoppers at high population densities. We observed that the effects of herbivory varied over time, most likely due to climatic variation. The northern Great Plains has a great deal of environmental variability in precipitation and temperature (Heitschmidt et al. 2005; Hansen & Wilson 2006), which can affect native plant establishment in Crested wheatgrass areas (Bakker et al. 2003; Hansen & Wilson 2006). As a result, the low species diversity in all plots in 2004 could have resulted from reduced precipitation or the early senescence of native plant seedlings prior to sampling. The fact that we observed a significant year effect on abundance, species richness, and Shannon diversity highlights the underlying effects that climatic variation is likely to have on the plant community-level impact of grasshopper herbivory.

The results of this study could be interpreted to indicate that controlling grasshoppers with pesticides might be warranted as part of a Crested wheatgrass area restoration program. However, there are numerous ecological and environmental issues that can arise from large-scale grasshopper control efforts (Branson et al. 2006). In addition, grasshoppers make numerous positive contributions to grassland ecosystem function such as accelerating nutrient cycling and providing food for many other organisms (McEwen & DeWeese 1987; Belovsky & Slade 2000). If additional research demonstrates that grasshoppers negatively influence the desired management outcomes in Crested wheatgrass-dominated areas, ecologically based approaches may be feasible to reduce grasshopper numbers. For example, livestock grazing and fire may be practical ways to help manage grasshopper numbers although potentially promoting restoration of native species (Grace et al. 2001; Branson et al. 2006). Given the highly variable nature of grasshopper population dynamics, another alternative to direct grasshopper control would be to monitor grasshopper population densities and implement restoration activities during time periods when grasshopper densities were low.

These findings illustrate the importance of understanding the impact of abundant invertebrate herbivores on the

relationships between exotic and native plants. There is increasing evidence that grasshopper herbivory can influence plant community composition (Thompson et al. 1996; Belovsky & Slade 2000) and should be considered when developing management plans for prairie restoration. Specifically, herbivory by generalist grasshoppers may place additional constraints on the restoration of Crested wheatgrass-dominated areas. Because Crested wheatgrass is a strong competitor and may alter soil chemistry (Christian & Wilson 1999), the additional stress to native species from grasshopper herbivory might increase the likelihood that native plants become eliminated from some areas. Grasshopper population dynamics are notoriously variable, however, leading to correlated temporal variation in herbivory pressure (Belovsky 2000; Joern 2000; Branson et al. 2006). Furthermore, grazing by vertebrates may have positive effects on native plants that enable them to persist despite the negative effects of grasshopper herbivory (Wilson & Pärtel 2003; Hansen & Wilson 2006). As a result, it seems unlikely that Crested wheatgrass monocultures are a direct consequence of long-term grasshopper herbivory. Although grasshopper herbivory negatively affected native plants in this study, it is important to recognize the simultaneous and interactive roles of vertebrate herbivory and the competitive effects of Crested wheatgrass on native plants.

Implications for Practice

- Grasshopper herbivory negatively affected the species richness, abundance, and Shannon diversity of native plants in 3 of 4 years in a Crested wheatgrass-dominated grassland.
- When abundant, generalist feeding grasshoppers could tilt the balance against the establishment of native plants during efforts to restore Crested wheatgrass sites to native grasslands.
- The impact of abundant native invertebrate herbivores should be considered when developing management plans for prairie restoration.

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